

STUDIES IN THE CAPPARIDACEAE II.<sup>1</sup> THE MEXICAN SPECIES OF CLEOMELLA: TAXONOMY AND EVOLUTION

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The Mexican species of *Cleomella*, a small North American genus of the Capparidaceae, are poorly known despite the fact that the genus was recently monographed by Payson (1922) and has received some attention since by West Coast floristic workers. During the preparation of a treatment of the Capparidaceae of Nevada (Iltis, 1955) and a phylogenetic study dealing with some North American Cleomoideae (Iltis, 1956), many specimens of *Cleomella* were examined. In the present study, a new species (*Cleomella perennis*) is described, the already-described taxa are more accurately delimited, some nomenclatorial problems are clarified, and certain aspects of the evolution of the taxa are discussed.

An examination of the specimens labelled *C. longipes* Torr. at the United States National Herbarium revealed that these could be separated easily into two groups on the basis of both morphological characters and geographic distribution. The specimens from the area including northern Mexico (Chihuahua), southwestern Texas, and southeastern Arizona (*C. longipes* Torr., *sensu stricto*) are all rather robust annuals with an erect stem or leader and with relatively large leaves, while those from Durango, Zacatecas, San Luis Potosí and Guanajuato in central Mexico (*C. perennis*) are all perennials with strongly thickened caudices, slender, decumbent or ascending branches, much smaller, narrower leaves, and fewer-seeded silicles. Despite these rather marked differences, the northern and southern populations have been classified under the same name for over one hundred years, largely because the shape of the fruit and length of the gynophore are nearly identical, two criteria usually of critical importance in other Cleomoideae. The only other Mexican species, the rare *Cleomella mexicana* Moc. & Sessé in DC., of the south-central Mexican plateau, is easily distinguished from its two northern relatives by its very short gynophore, small leaves, and prostrate branches. As was recognized by de Candolle (1824), it, too, is perennial, with a woody caudex and rootstock which is well illustrated in the "type-drawing" (cf. p. 182). This condition, occurring in two out of the three Mexican species of *Cleomella*, was completely overlooked by Payson (1922), who considered all species of the genus as annuals.

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## I. TAXONOMY

CLEOMELLA DC. Prodr. 1:237. 1824. (Type: *C. mexicana* Moc. & Sessé in DC.). *Isopara* Raf. Atl. Jour. 1:144. 1832. (Based on *C. mexicana* Moc. & Sessé in DC.). *Hyponema* Raf. Good Book 40. 1840. (*nom. nov.* *Cleomella* DC. 1824). *Cleome* sect. *Cleomella* (DC). Baill. Hist. Plant. 3:149. 1872.

Erect to decumbent, unarmed, slender to robust, annual or perennial herbs, glabrous (except *C. obtusifolia*). Leaves 3-foliolate; leaflets entire, mucronulate, less than 4 cm. long, more or less thick, stipulate, the stipules minute, hyaline, filiform, usually less than 3 mm. long. Racemes terminal, usually bracteate, the bracts either 1-foliolate or the lower 3-foliolate, or flowers borne singly in the axils of cauline leaves. Sepals very small, free or basally connate, tardily deciduous. Corolla closed (convolute) in the bud; petals yellow, sessile or subsessile. Disk small, frequently expanded adaxially. Stamens 6, the anthers tightly coiled when dry. Fruit a small obdeltoid, rhomboidal, deltoid or ovoidal silicle, usually wider than long, often compressed contrary to the placenta, the valves usually conical. Silicles borne on short to elongate gynophores, the indurate, persistent styles usually setulose. Seeds 2–12 (–19) in each silicle, free-falling, the two claws formed by the invagination of the testa fused nearly their whole length, with only a trace of an internal sinus between them; testa usually smooth and often delicately marked (colliculate).

A genus with ten species, endemic to the western United States and Mexico; very closely related to *Cleome* sect. *Peritoma* (DC.) Baill., from which it differs principally in the smallness and shape of the fruit.

## KEY TO THE MEXICAN SPECIES OF CLEOMELLA

- A. Leaflets of principal leaves 15–30 mm. long, 3–10 mm. wide; plants annual, from a usually slender taproot, with a branched or unbranched main stem (leader) usually simple at the base, the branches strongly ascending; Chihuahua to southwestern Texas and southeastern Arizona.....1. *C. longipes*
- AA. Leaflets of principal leaves 5–14 mm. long, 1–5 mm. wide; plants perennial, much branched at the base from a greatly thickened, short woody root and caudex, the branches ascending to decumbent or procumbent.
  - B. Gynophore of fruit 11–16 mm. long; seeds 2.2–2.6 mm. long; branches ascending to decumbent, to 7 dm. long, the plants up to 5 dm. tall; Durango to San Luis Potosí and Guanajuato.....2. *C. perennis*
  - BB. Gynophore of fruit 0.4–2.0 mm. long; seeds 1.9–2.0 mm. long; branches decumbent or prostrate, to 3 dm. long, the plants rarely over 1 dm. tall; Mexico, D. F. and northern Pueblo .....3. *C. mexicana*

1. CLEOMELLA LONGIPES Torr. in Hook. Jour. Bot. & Kew Gard. Misc. 2:255. 1850; in Gray, Plantae Wrightianae 1:11. 1852 [Smithson. Contr. Knowledge 3 (Art. 5):11], *pro parte*, including the lectotype, *Gregg 5441*; excluding the *Gregg* San Luis Potosí specimen [herein cited under *C. perennis* Iltis].

Robust, glabrous, erect annual from an usually unbranched or little-branched taproot, 3–8 dm. tall, unbranched or more frequently with sev-

eral, strongly ascending branches, these usually scattered above the lower one-fourth of the erect main stem (leader), with only few branchlets, the main stem 2–6 mm. in diam.; petioles 7–30 mm. long, the petiolules 1–2 mm. long; leaflets oblanceolate to oblong-oblanceolate, acute to rounded or rarely emarginate, attenuate to the base from near the middle, 15–30 mm. long, 4–10 mm. wide, flat or conduplicate; racemes well defined, dense, greatly elongating in fruit, to 30 cm. long, bracteate or the upper portion ebracteate, the bracts 3-foliolate below, unifoliolate and reduced above; sepals connate at the base, triangular-lanceolate, acuminate to caudate-acuminate, 1.5–2.5 mm. long, tardily deciduous; petals oblong or lanceolate-oblong, obtuse to rounded, usually abruptly contracted into a short claw (5–)6–9 mm. long, 2–3 mm. wide; staminal filaments 8–12 mm. long; anthers 2.0–3.5 mm. long; ovary exerted on long gynophore; mature silicles obdeltoid to rhomboidal, 4–7 (–11) mm. long, 6–12 mm. wide, the style 1–2 mm. long; gynophore (6–)10–17(–21) mm. long, usually yellowish; pedicel (5–)7–15(–18) mm. long; seeds (4–)8–16 (–19) in each silicle, obovoidal, 1.9–2.4 mm. long, 1.4–2.0 mm. wide, 1.0–1.2 mm. thick, when mature dark brown, with the prominent lip of the shorter claw yellowish.

Chisos Mountains of southwestern Texas to the Chiricahua Mountains of southeastern Arizona, south to southern Chihuahua, Mexico, at elevations of 2500–5000 feet, in saline, alkaline soils or sands of semi-deserts, at edges of playas, old lake beds, thickets, ravines, and valleys, sometimes in *Tamarix-Prosopis* association, flowering and fruiting from late April to late September.

UNITED STATES: ARIZONA. County unknown: *D. T. McDougal, s. n.* (US).<sup>2</sup> Cochise County: west of the Chiricahua Mountains, *Wright 857* (MO); 3 miles west of Willcox, *Darrow, Phillips & Pultz 1045* (US). NEW MEXICO. Hidalgo County: Dog Spring, Dog Mountains, *Mearns 2379* (US), *Hershey s. n.* (ILT, NMC). TEXAS. County unknown: Near J. Davis' ranch, West Texas, *Havard 135* (US). Brewster County: Chisos Mountains area, in ravine of Rio Grande valley, *Sperry 136* (US); near Chisos Mountains, *Young 101* (MO); Rio Grande valley near Terlinguas, *Palmer 34215* (MO); 3 miles southeast of Chilocal Mountain, *Marsh s. n.* (F). Hudspeth County: Rio Grande near Indian Hot Springs, *Waterfall 4856* (MO). Presidio County: Penitas Ranch, 24 miles south of Marfa, *Hinckley 1050* (F); near Chinati Mountains, *Hinckley 824* (F). MEXICO. CHIHUAHUA. Near San Pablo, April 29, 1847, *Gregg 544* (MO); Rio Palotat near Janos, *Schott s. n.* (F); Casas Grandes, *Goldman 436* (US); Colonia Diaz, *Nelson 6434* (US).

Torrey, in his original description of *C. longipes*, lists only two specimens, both collected by Dr. Gregg, one from Chihuahua and the other from San Luis Potosí. In the Missouri Botanical Garden Herbarium there are three Gregg collections, all of which can be considered isotypic, two of 544 labeled as from Chihuahua and clearly belonging to the northern taxon (*C. longipes sensu stricto*) and a third without any data except the

<sup>2</sup> The herbarium abbreviations used in the species citations, except for ILT, which refers to specimens in my own study collection, are those proposed by Lanjouw and Stafleu, *Index Herbariorum, Regnum Vegetabile* 2<sup>1</sup>:106–117. 1952.

collection number (579). The latter is evidently the specimen from San Luis Potosí mentioned by Torrey, for it agrees in every respect with the other collections from that state, which belong to the southern entity mentioned in the introduction (*C. perennis*). Torrey thus established *C. longipes* on two collections belonging to two distinct though closely related taxa. His very generalized description offers no clue as to which of the two collections was primarily used by him in establishing *C. longipes*. Payson (1922), in his revision of *Cleomella*, likewise did not distinguish between the two taxa included in Torrey's *C. longipes*, undoubtedly because of the small number of specimens available to him for study. He did, however, choose the Chihuahuan Gregg collection as the lectotype, thus permanently associating the name *Cleomella longipes* with the plants from north-central Mexico and the adjoining United States. Kearney and Peebles (1942, p. 373) cite Wright 857, from the Chiricahua Mountains, as the type of *C. longipes*. This is an error, for the specimen was not cited by Torrey in the original description.

The specimens from the Chisos Mountains, the easternmost station of *C. longipes*, apparently represent a local race characterized by wider, emarginate leaflets, stronger connation of sepals, shorter anthers, and lower number (4–5) of seeds, which are larger than average.

2. *Cleomella perennis* sp. nov. Herbae glabrae vel minutule papillosae, perennes basi ramosae e caudice lignoso crasso; rami annui plus minusve suffruticosi, interiores erecti et ca. 15–50 cm. alti, exteriores decumbentes adscendentes, longitudine ad 70 cm.; folia densa, petiolis brevibus (2–10 mm.); foliola oblanceolata-cuneata 5–14 mm. longa, 1–4 mm. lata, apice rotundato vel emarginato; bractae racemi uni- vel trifoliolatae, superne graduatim decrescentes; petala spatulata, 4.5–7.2 mm. longa, sepala triplo superantia; stamina et ovarium corollam duplo superantia; siliculae maturae obdeltoideae vel deltoideae, 6–12 mm. latea; gynophorum gracillimum 11–16 mm. longum; semina subgloboso-reniformia, 2.2–2.6 mm. longa, 1.7–2.2 mm. lata, 3–7 per siliculam.

Holotypus. *C. G. Pringle*, Plantae Mexicanae 3089, in U. S. Nat. Herb. No. 1418485 ("Saline Plains, Salinas, San Luis Potosí, Mexico, June 30, 1890"). Isotypi in Herb. BR, F, ILT, MO, MSC, SMU, et W.

Slender, more or less suffruticose and bushy, glabrous or minutely papillose perennial herbs, much branched mainly from the apex of the greatly thickened, woody caudex (short and to 2 cm. in diam.) the clustered and branched annual stems 1–2 (–3) mm. in diam., the inner erect and 15–50 cm. tall, the outer ascending to decumbent and up to 70 cm. long, densely leaved and frequently with many, very short branchlets; petioles 2–10 mm. long; petiolules 1 mm. long or less; leaflets narrowly oblanceolate-cuneate, rounded to emarginate, mucronulate, gradually attenuate to the base from near the apex, 5–12 (–14) mm. long, 1–5 mm. wide, usually strongly conduplicate; racemes well-defined, dense, greatly elongating in fruit, up to 25 cm. long; lower bracts trifoliolate and like the foliage leaves, much reduced and either trifoliolate or unifoliolate



above; sepals joined at the base, broadly to narrowly triangular, acuminate to caudate-acuminate, 1.3–2.2 mm. long, tardily deciduous; petals oblong to lanceolate-oblong or oblanceolate, obtuse, gradually tapering to the base, 4.5–7.2 mm. long, 1.8–2.8 mm. wide; staminal filaments 10–14 mm. long; anthers 1.6–2.7 mm. long; ovary exserted on long gynophore; mature silicles obdeltoid, rhomboidal or deltoid, (3–)5–7 mm. long, 6–12 mm. wide; style 0.9–1.5 mm. long; gynophore 11–16 mm. long, usually dark purplish; pedicel 7–14 mm. long; seeds (3–)5–7 in each silicle, broadly obovoidal to subglobose, 2.2–2.6 mm. long, 1.7–2.2 mm. wide, 1.3–1.7 mm. thick, when mature brown to brownish-black, sometimes mottled, shiny, with the usually prominent lip of the shorter claw yellow-brown to whitish.

Mexico, from central Durango east to central San Luis Potosí and northern Guanajuato, at elevations near 6000 feet, in saline plains, ciénega bottomlands in grama grasslands (Gentry), steppes, ditches in grassy plains, and in sunny uncultivated fields; flowering and fruiting from late June into October (December).

MEXICO. DURANGO. City of Durango and vic., *E. Palmer 1896–326* (F, ILT, MO, US); 40 miles north of Ciudad Durango, *Gentry 8587* (US). ZACATECAS. 9 miles south of Villa de Cos, on road from Sierra Hermosa southwest to Zacatecas, *Johnston 7437* (F, US), *Shreve 8623* (US). SAN LUIS POTOSÍ. Salinas, *Pringle 3089* (BR, F, ILT, MO, MSC, SMU, US type, W); Charcas, *Lundell 5587* (US); San Francisco, *Gregg 579* (MO, cited by Torrey as *C. longipes*). GUANAJUATO. Jaral, *Schuman 311* (ILT, M, US) *Schnee s. n.* (ILT, P).

The Pringle collection was chosen as the type because of the widely distributed isotypes and the excellence of the material which includes not only flowers and nearly mature fruits, but also well developed caudices, so often left behind by most "hay-baling" collectors. Its bracts are 1-foliolate. Palmer's Durango collection, also widely distributed, supplements the type by its mostly 3-foliolate bracts and fully mature seeds and fruits. The two collections from Zacatecas cited above have unusually large caudices.

*Cleomella perennis* is intermediate between, and very closely related to, the preceding and following species geographically as well as morphologically. Thus the fruit and gynophore are nearly identical with those of *C. longipes*, the caudex and leaves with those of *C. mexicana*. In habit, size, erectness and most other attributes, *C. perennis* is exactly intermediate. Only the larger seeds and the lower seed number are out of line. As will be discussed presently, it is probable that *C. longipes* gave rise to *C. perennis*, which in turn is ancestral to *C. mexicana*.

3. CLEOMELLA MEXICANA Moc. & Sessé in DC. Prodr. 1:237. 1824; A. DC. Calq. Dess. Fl. Mex. Moc. & Sessé, t. 19. 1874. *Isopara mexicana* (Moc. & Sessé in DC.) Raf. Atl. Jour. 1:144. 1832. *Cleome mexicana* (Moc. & Sessé in DC.) D. Dietr. Syn. Pl. 2:1068. 1840, non *Cleome mexicana* Hemsl. Bio. Centr. Amer. Bot. 1:41. 1879.

*Cleomella medicagineae* Turcz. in Bull. Soc. Nat. Mosc. 27<sup>2</sup>:313. 1854, ex char. (Type: Galeotti 7216). *Physostemon medicagineum* (Turcz.) Briqu. in Ann. Conserv. & Jard. Bot. Genève, 17:390. 1914.

Slender, herbaceous or somewhat suffruticose perennials from a stout taproot and caudex, 1–2 dm. tall, profusely branched, particularly from the base, the clustered branches strongly decumbent, 10–25 cm. long, 1–2 mm. in diameter; petiole 5–13 (–19) mm. long; petiolules 1 mm. long or less; leaflets thick, cuneate-obovate, truncate to emarginate, gradually attenuate to the base from above the middle, 3–11 mm. long, 2–5 mm. wide, strongly conduplicate; racemes lax and ill-defined, not greatly elongating in fruit, the flowers borne near the tip of the branches in the axils of full-sized or slightly reduced 3-foliolate leaves; sepals barely joined at the base, lanceolate, acuminate, 1.3–1.7 mm. long, deciduous; petals broadly oblanceolate, rounded, gradually attenuate to a broad base, 3.5–4.2 mm. long, 1.5–1.9 mm. wide; stamens included, the filaments 2–3 mm. long; anthers 1.2 mm. long; ovary included; mature silicles obdeltoid to rhomboidal, 3–5 mm. long, 6–9 mm. wide; style 0.3–0.5 mm. long; gynophore 0.4–2.0 mm. long, purplish; pedicel 8–11 mm. long; seeds 6–8 (–10?) in each silicle, obovoidal, 1.9–2.0 mm. long, 1.5–1.6 mm. wide, 1.1–1.2 mm. thick, brown, the lip of shorter claw not conspicuous.

In saline plains, in the vicinity of Mexico City and Tepeyahualco, Pueblo, at elevations of 7000–7700 feet, flowering and fruiting from May to late September (December).

MEXICO. *Sessé, Mociño, Castillo & Maldonado 3356* (MA); between Vera Cruz and Mexico City, *Halstead s. n.* (MO). MEXICO, D. F. Mexico City, *Rutten & Rutten-Pekelharing 438* (ILT, U). PUEBLO. Prope Tepeyahualco, *Schiede & Deppé s. n.* (M.).

*Cleomella mexicana*, the type of the genus, is fairly well illustrated in Sessé and Mociño's unpublished "Icones Florae Mexicanae," which were copied by the ladies of Geneva for the elder de Candolle before the plates had to be returned to Madrid (cf. Standley, 1920, p. 16). Tracings of these copies (A. de Candolle, 1874) are in the library of the Missouri Botanical Garden, *Cleomella mexicana* being plate 19. A Macbride photograph (No. 30454) of the original water color copy now at Geneva is in the herbarium of the Chicago Natural History Museum. Since the only thing de Candolle had at hand when he described the species was this Sessé and Mociño plate, it must be taken in lieu of the type. However, in the Instituto Botánico "Antonio José Cavanilles," Madrid, there is a sheet with abundant specimens of *Cleomella mexicana* collected by Sessé, Mociño et al.

Judging from the description, *Cleomella medicaginea* Turcz. is clearly the same as *C. mexicana*. It is based on a collection of Galeotti's from "planitie salsa prope urbem Mexico." *Cleomella medicaginea* was later transferred by Briquet (1914, p. 390) to *Physostemon* (as *P. medicagineum*), a quite unrelated group, because he thought Turczaninow's species to be identical with Hemsley's *Cleome mexicana* (1879), and wanted

to conform to the rules of priority, for Hemsley's *Cleome mexicana* indeed does belong to *Physostemon*, a *Cleome* segregate with unifoliolate leaves and apophysate stamens.<sup>3</sup>

The exact localities where *Cleomella mexicana* has been collected have never been cited with the collections. It is almost certain though that the "salt-lake" Lago de Texcoca (alt. 2236 m.), east of Mexico City, which was drained in 1920, was the location for the specimens labelled as coming from Mexico City, and that the series of large salt-flats south and southwest of Tepeyahualco are likewise the origin of the collection labelled as coming from that town. As a matter of fact, these are the only saline lakes reported on the *Hoja Puebla* (lat. 19°N., long. 97° 30'W.) topographic map (1:500,000; 1944) of the *Dirección de Geografía, Meteorología e Hidrología* of Mexico.

## II. PHYLOGENY

Evolution in the subfamily Cleomoideae seems to have progressed in many instances from types inhabiting mesic habitats to those growing in deserts or semi-deserts. Certain recurrent evolutionary trends represent not only evolution from the more primitive to the specialized morphological type but, more specifically, the evolution of structures more closely in harmony with arid and/or alkaline habitat requirements. Similar trends occur in the New World not only in *Cleomella* but also in quite unrelated groups of species (e.g., the unifoliolate species of *Cleome*, including *Physostemon*), as well as in various groups of the Old World.

The following list of evolutionary tendencies in the Cleomoideae applies mainly to the genus *Cleomella*, especially the Mexican species, but would hold true for all its close relatives (viz. *Cleome* sect. *Peritoma*, *Wislizenia*, *Oxystylis*) and, with a little modification, for most other xerophytic Cleomoideae as well. Some of these conclusions are at variance with present day phylogenetic points of view. A full explanation of the reasons for considering characters primitive or specialized in the Western North American Cleomoideae (exclusive of *Polanisia*) are given in a forthcoming study (Iltis, 1956) dealing with the morphology and phylogeny of the species of *Cleome* Section *Peritoma*, *Cleomella*, *Wislizenia*, and *Oxystylis*. In Table 1 characters that occur in *Cleomella longipes* are indicated by (1), those that occur in *C. perennis* by (2) and in *C. mexicana* by (3).

<sup>3</sup> Hemsley's *Cleome mexicana* of 1879 (in *Biologia Centrali-Americana*, Botany 1:41) was invalid because preoccupied by *Cleome mexicana* (Moc. & Sessé in DC.) D. Dietr. 1840. (= *Cleomella mexicana*). To correct this, Bullock (in *Kew Bull. Misc. Inf.* 1936:388) renamed Hemsley's species *Cleomella hemsleyana* Bullock, thus assigning it to the wrong genus. To place this taxon among its relatives, Foster (in *Contr. Gray Herb.* 155:58. 1945) transferred it to *Physostemon* [as *P. hemsleyanum* (Bullock) Foster]. In my opinion, it is not possible to segregate *Physostemon* from the unifoliolate New World species of *Cleome*. It therefore becomes necessary to return the invalid *Cleome mexicana* Hemsley to *Cleome* as *C. hemsleyana* (Bullock) Iltis, comb. nov. (Type: *Galeotti 3194*, K !).

TABLE 1. COMPARISON OF PRIMITIVE AND SPECIALIZED CHARACTERS IN MEXICAN SPECIES OF CLEOMELLA AND RELATED TAXA

A. Primitive	B. Specialized
1. Annual with little branched taproot. (1)	Perennial with roots from a woody caudex or rootstock. (2-3)
2. Plants large (1-6 m.).	Plants small (1-100 cm.). (1-3)
3. Stems simple at the base with unbranched main leader. (1)	Stems much branched from the base without a main leader. (2-3)
4. Stems erect or strongly ascending. (1-2)	Stems decumbent to prostrate. (2-3)
5. Leaves estipulate.	Leaves with minute "stipular" structures. (1-3)
6. Leaves large, 3- to 13-foliolate. (1)	Leaves small, 3- or 1-foliolate. (1-3)
7. Leaves long-petioled. (1, 3)	Leaves short-petioled to sessile. (2-3)
8. Leaflets at apex caudate-acuminate to acute, at base long-attenuate. (1)	Leaflets obtuse to emarginate at apex, cuneate to rounded at base. (1-3)
9. Leaflets lanceolate-elliptic. (1)	Leaflets oval to obovate. (1-3)
10. Leaflets thin, with many raised lateral nerves.	Leaflets thick, with only the midrib and few immersed, nearly obsolete lateral nerves. (1-3)
11. Leaflets more or less flat. (1)	Leaflets strongly conduplicate. (2-3)
12. Flower and fruit production after much vegetative growth. (1-2)	Flower and fruit production after little vegetative growth. (2-3)
13. Racemes bracteate. (1-3)	Racemes ebracteate. (rarely in 1)
14. Flowers in well defined terminal racemes. (1-2)	Flowers in the axils of cauline leaves (associated with 4B). (3)
15. Bracts 1-foliolate. (1-2)	Bracts 3-foliolate or like cauline leaves. (2-3)
16. Post-floral elongation of raceme axis very pronounced.	Post-floral elongation of raceme axis small.
17. Nectary small, smooth.	Nectary relatively large, variously sculptured, etc. (1-3)
18. Petals large. (1-2)	Petals small. (3)
19. Stamens and ovary long-exserted. (1-2)	Stamens and ovary included or nearly so. (3)
20. Stigma large, capitate, sessile.	Stigma minute, truncate or pointed, on slender style. (1-3)
21. Fruits terete, linear-cylindric, large and long (5-25 cm.), many-seeded.	Fruits compressed, various, small and short (1-3 cm. or less), few-seeded. (1-3)
22. Fruits with deciduous valves, and free-falling seeds. (1-3)	Fruits with persistent valves separating only at apex, or with valves that permanently enclose seeds.
23. Gynophore long. (1-2)	Gynophore short. (3)
24. Seeds with large internal sinus.	Seeds with obsolete internal sinus. (1-3)

The somewhat unusual conclusion that the perennial woody caudex of the Cleomoideae is a derived or specialized structure is based primarily on the fact that in the Mexican species of *Cleomella*, where all traits except for minor exceptions (see below) follow interrupted clines from north to south, all of many characters (except for the problematic one of duration) are in the primitive state in the northern *C. longipes*, in the special-



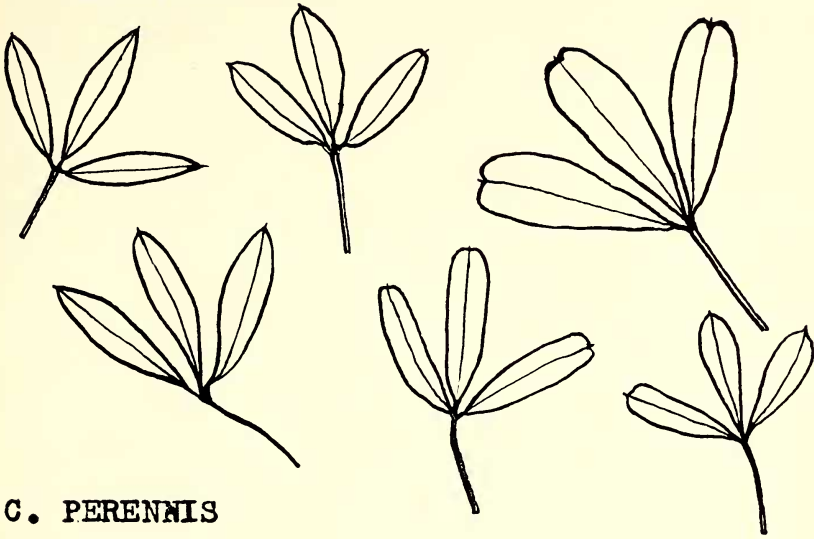
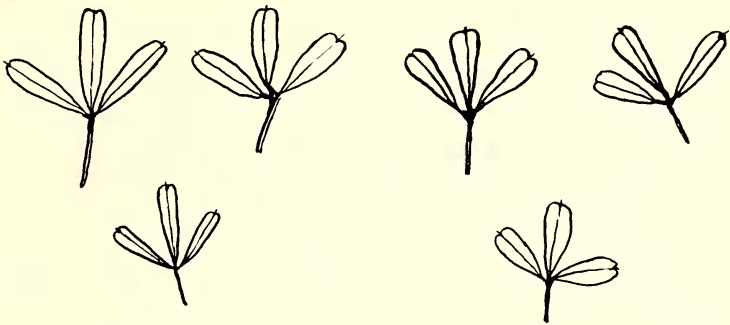
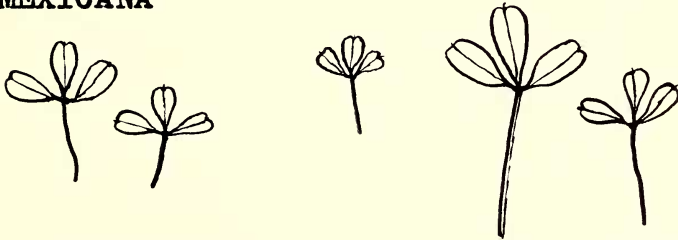
**C. LONGIPES****C. PERENNIS****C. MEXICANA**

FIG. 1. Principal cauline leaves of the Mexican species of *Cleomella*. Natural size.

ized state in the southern *C. mexicana*, while the geographically intermediate *C. perennis* is morphologically intermediate also (cf. figs. 1 and 2). Secondly, the reputed ancestors of *Cleomella* (see below) are all annuals. Thirdly, parallel situations exist in *Wislizenia* (Greene, 1906) and in

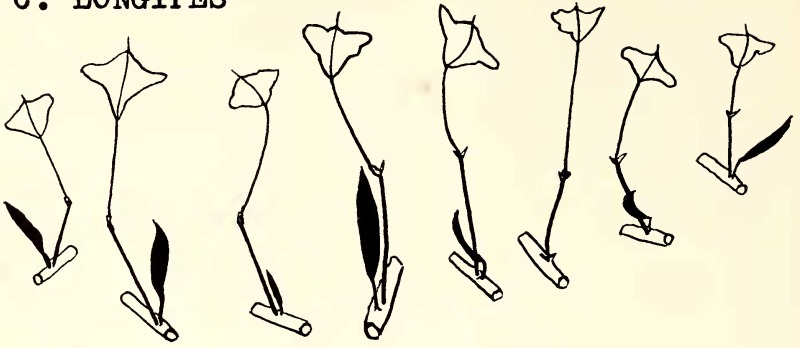
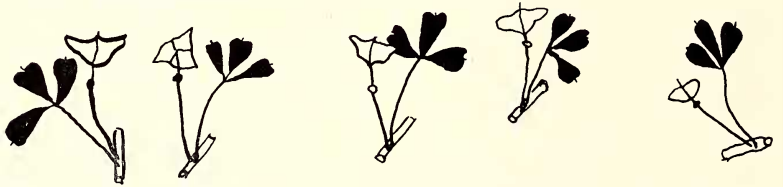
**C. LONGIPES****C. PERENNIS****C. MEXICANA**

FIG. 2. Mature silicles and bracts of the Mexican species of *Cleomella*. Natural size. Each fruit from a different collection, except the lower left two, where the first shows the usual dimerous silicle, and the second the rare, abnormal trimerous fruit.

several groups quite unrelated to *Cleomella* which leave little doubt that in certain arid climes evolution may proceed from the annual to the perennial habit. For example, in the phyletic sequence of the unifoliolate Cleomoideae (and relatives) of the New World, the primitive taxa (*Cleome tenuis*, *C. stenophylla*) are annuals, while the more specialized forms had evolved the perennial habit in at least two separate lines: 1) in the West Indian semi-desert species (*C. wrightii*, *C. macrorhiza*, etc.) and 2) in the highly specialized taxa commonly classified under the genus *Physostemon*, which are native to the arid "Caatinga" of northeast Brazil and to the southern Mexican grasslands.

Therefore, the perennial woody rootstock of these plants which, according to Bessey (1915) and other workers, would indicate a primitive structure, must be thought of rather as a derived condition which had developed in the arid, alkaline inter-montane plateau region of central and southern Mexico, and in climatically similar regions, as an adaptation to that particular habitat type, a development which occurred in various groups at various times through convergent evolution.

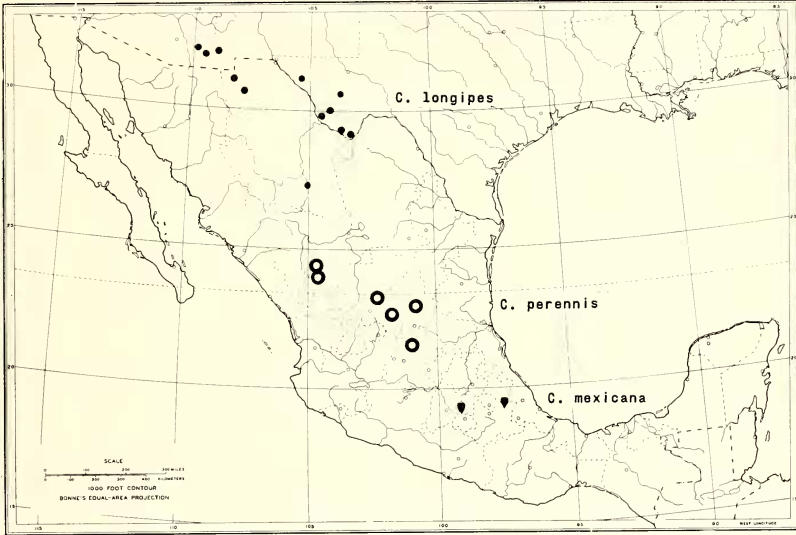


FIG. 3. Distribution of the Mexican species of *Cleomella*. (Base map Goode's copyrighted map 112 with permission of the University of Chicago.)

We can detect only two minor exceptions to the uniformly north-south sequences of nearly all morphological modifications: 1) in seed size, that of *C. perennis* being greater on the average than that of either of the two other species, and 2) in petiole length, the petioles of *C. perennis* being often shorter than those of either *C. longipes* or *C. mexicana*.

From this evidence, it seems reasonable to assume that in Mexico *Cleomella* migrated from north to south (fig. 3). To emphasize this, it should be pointed out that *Cleomella* as a genus is clearly derived from *Cleome* sect. *Peritoma* (DC.) Baill., of which the annual, erect, 5-foliolate *Cleome lutea* of the western United States is probably most like the ancestor of *Cleomella*. *Cleomella angustifolia* of eastern Texas and Oklahoma, a tall, erect, 3-foliolate annual, is very similar to *Cleome lutea*, particularly vegetatively. It is also very similar to *Cleomella longipes*, allopatric to the southwest, but has more acute, larger leaflets and larger, rugose seeds. These two appear to be the most primitive of all the 10 species of *Cleomella*.

The allopatric distribution of the Mexican taxa (fig. 3) also supports the belief that these three species of *Cleomella* are part of a single phylad

that originated in the Arizona-Texas region and migrated southward from there. This appears to me to be of considerable interest since the species of *Cleomella* are a typical part of the southwestern desert flora, the members of which are reputed to have migrated *north* from the Mexican plateau (Munz, 1935). While this has undoubtedly occurred in the case of the ancestors of the more primitive *Cleome* sect. *Peritoma*, the northward migration (at least here) was followed at a later and perhaps rather recent date by a southward migration of some of its more specialized descendants, namely the Mexican species of *Cleomella*.

Two additional north-south trends are found in the Mexican species of *Cleomella*. One, the tendency for a southward decrease in distributional area is evidenced here by *C. mexicana*, the southernmost of the species of *Cleomella*, as compared with the more northern species (fig. 3). It occurs in the only two available saline areas in the region around Mexico City. Because of this narrow ecological restriction, it might be considered homogenic (Stebbins, 1942). The second north-south trend is evidenced by the fact that the species of *Cleomella* occur at progressively higher altitudes towards the south: the northern *C. longipes* occurring at elevations of 2500–5000 feet, the central *C. perennis* at about 6000 feet, and the southern *C. mexicana* at 7000–7700 feet. This corresponds to the fact that given vegetational zones occur at higher elevations in lower latitudes.

### III. SUMMARY

A new perennial species of *Cleomella* (*C. perennis*) is described from north-central Mexico. It is closely related to and intermediate between *C. longipes* to its north, an annual with larger leaves, and *C. mexicana* to its south, a perennial with low decumbent branches and smaller flowers. A preliminary list comparing primitive versus specialized characters in the Cleomoideae is presented, and the view is proposed that the perennial habit may, in some cases, be the specialized rather than the primitive condition. All data support the contention that *C. longipes* is most primitive and has given rise to *C. perennis* and *C. mexicana*. These species comprise a phylad which probably had a northern origin and a southward migration. Since the group ancestral to *Cleomella* (*Cleome* sect. *Peritoma*) originated from tropical stock that moved north to the region of the southwestern United States, the Mexican branch of *Cleomella* thus returned to Mexico on the route of its ancestors, but probably in drier habitats and at higher elevations. The southwestern desert flora which generally is considered to have originated from the flora of the semi-arid Mexican plateau, thus seems to have returned the favors to the latter by the contribution of some of its specialized, more recent derivatives.

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## TWO FUNGI ASSOCIATED WITH A MICROCYCLIC RUST, COLEOSPORIUM CROWELLII CUMMINS, ON NEEDLES OF PINUS EDULIS ENGELM. IN ARIZONA<sup>1</sup>

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The microcyclic rust, *Coleosporium crowellii* Cummins (Cummins, 1938) is unique among species of the genus because of the occurrence of the telial stage on species of *Pinus*. This species of *Coleosporium* is also regarded as autoecious. Other species of *Coleosporium* are macrocyclic with needles of certain pines serving as sites for the pycnia and aecia rather than the telia. In addition, species of *Coleosporium* are generally heteroecious.

Material of *C. crowellii* on *Pinus edulis* Engelm. was collected one mile east of Yaki Point, on the north side of State Highway 64 along the South Rim of the Grand Canyon, Grand Canyon National Park, Coconino County, Arizona, on October 6, 1953. The telial sori were of an unnatural dull yellow-brown, rather than the usual yellow-orange. The sori of the rust fungus were found to be invaded by two non-uredineous fungi, *Darluca filum* (Biv.) Castagne and *Cladosporium aecidiicola* Thüm. Both of the fungi were in their conidial phases. No previous reports of these two hyperparasites on this rust have been found.

Materials for microscopic examination were prepared in the following manner: small portions of pine needle tissue containing rust sori invaded

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